

STOPOVER OF NEOTROPICAL LANDBIRD MIGRANTS ON EAST SHIP ISLAND FOLLOWING TRANS-GULF MIGRATION¹

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Abstract. The ecophysiology of Neotropical landbird migrants was studied in relation to energetic condition following trans-Gulf migration in 1987, 1988, and 1989. Most birds captured on East Ship Island, a barrier island off the Mississippi coast, had exhausted fat reserves crossing the Gulf of Mexico and were near fat-free mass. Few birds were recaptured after the day of their first capture, suggesting that migrants departed the day of their arrival or that night. Lean migrants occurred more frequently in samples of recaptured migrants, although length of stay was not a clear function of arrival mass nor did change in mass simply increase with stopover length. Most species were characterized by loss of body mass or by rates of change that essentially maintained arrival mass during stopover. Rates of change in mass were positively correlated with energy demand for several species. Fat-depleted birds appeared to compensate for their condition, presumably by increasing their rate of energy acquisition. Estimates of prey abundance did not differ between years, which might explain why stopover length and rate of gain did not vary between years. We conclude that many migrants left ESI because they found few opportunities to satisfy energy demand, while others stayed because of constraints unrelated to their energy balance or because the benefits of rejecting the habitat were outweighed by the cost of finding a more suitable site.

Key words: *Migration; Neotropical landbird migrants; Gulf of Mexico; energetic condition; fat deposition.*

INTRODUCTION

During migration, birds cope with heightened energetic requirements at a time when contingencies decrease the certainty that energy demand will be satisfied (see Moore, in press). For example, migrants forage in unfamiliar locations that often bear little resemblance to breeding or wintering habitat (Martin 1980, Bairlein 1983, Hutto 1985a, Moore et al. 1990); they must resolve conflicting demands between predator avoidance and food acquisition (e.g., Metcalfe and Furness 1984, Lindström 1989), and compete with other migrants and resident birds for limiting resources (e.g., Hutto 1985b, Lindström and Alerstam 1986, Martin and Karr 1986, Moore and Yong 1991). At the same time, migrants must respond to unpredictable, sometimes unfavorable weather (Alerstam 1990). These problems are magnified when long-dis-

tance migrants negotiate a geographic barrier (see Moore and Kerlinger, in press). Yet, many small landbirds make long, nonstop flights over barriers during the course of their seasonal migrations (Alerstam 1981), and it is obvious that natural selection has favored these flights in spite of the risks and energy demands involved.

When Neotropical landbird migrants arrive along the northern coast of the Gulf of Mexico in spring, some individuals have mobilized their lipid reserves en route, are essentially fat-free and run the risk of a negative energy balance. Other birds retain sufficient fat to continue migrating the day of their arrival (e.g., Rappole and Warner 1976, Moore and Kerlinger 1987, Loria and Moore 1990). We examine the ecophysiology of Neotropical landbird migrants in relation to energy demand following trans-Gulf migration and consider the following expectations: (1) Stopover length is positively correlated with energy demand, i.e., lean, fat-depleted migrants delay departure longer than birds with unmobilized reserves (Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Safriel and Lavee 1988). (2) The expected relationship between arrival con-

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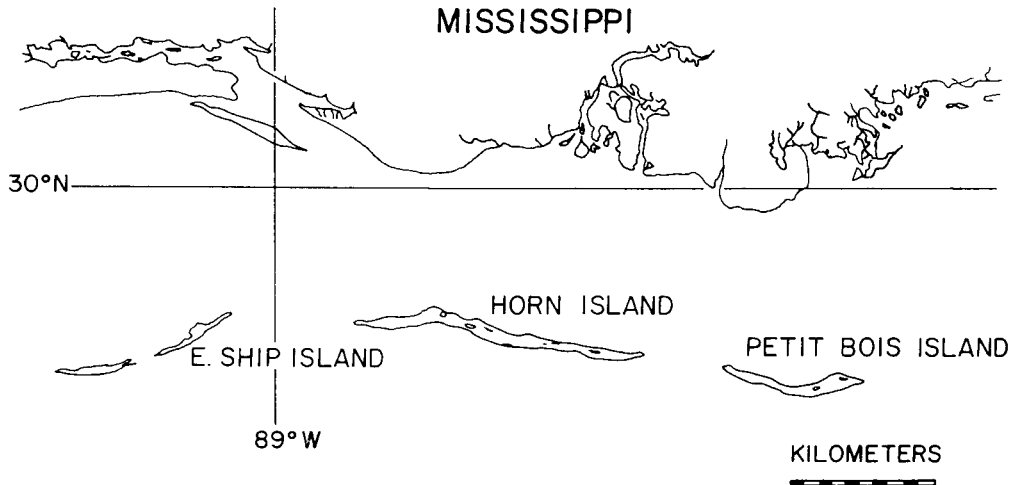


FIGURE 1. Study site located within a vegetated portion of East Ship Island, part of Gulf Islands National Seashore and one of the barrier islands that lay off the northern coast of the Gulf of Mexico.

dition and stopover length is predicated on the expectation that the longer a bird stays the more likely it will gain mass, i.e., change in mass during stopover is positively correlated with length of stay (e.g., Bairlein 1985, Biebach et al. 1986, Alerstam and Lindström 1990). (3) If the prospects for replenishing depleted reserves are related to the availability of food (see Hutto 1985a, Moore and Simons, in press), rates of fat deposition should be positively related to food availability (e.g., Graber and Graber 1983, Bibby and Green 1983). (4) If spring migrants are under strong selective pressure to minimize migration time (*sensu* Alerstam and Lindström 1990), lean, fat-depleted birds should compensate for their energetic condition and deposit fat at a faster rate than birds with unmobilized reserves (Loria and Moore 1990; Moore, in press).

STUDY AREA AND METHODS

STUDY LOCATION

East Ship Island (ESI), one of more than 50 barrier islands that border the northern Gulf of Mexico (Fig. 1), is included within Gulf Islands National Seashore, a unit of the National Park System established in 1971. The 250 ha island is 6 km long and lies approximately 19 km offshore. Our study site on ESI was a 5 ha relic dune bordered by marsh and slash pine (*Pinus elliotti*) and dominated by live oak (*Quercus geminata*), yaupon (*Ilex vomitoria*), and saw palmetto (*Sere-noa repens*). A detailed account of the vegetation on the island was published by Miller (1975).

CAPTURE/RECAPTURE PROTOCOL

Data were collected on 31 days between 27 March and 9 May 1987, on 45 days between 29 March and 14 May 1988, and on 40 days between 2 April and 12 May 1989 on ESI. Migrants were captured (and recaptured) using mist-nets (12 × 2.6 m, 30 mm mesh). Unless rain or high winds dictated otherwise, mist-nets were opened shortly after sunrise, usually closed during midday because of high temperatures and decreased shade, and opened again for a few hours in the afternoon. Body mass was estimated to the nearest ¼ g using a 50-g spring balance in 1987 and to the nearest 0.1 g in 1988 and 1989 using a digital electronic balance. Unflattened wing chord was measured, visible, subcutaneous fat deposits quantified according to a six-point scale developed by Helms and Drury (1960), and birds banded with a USFWS aluminum leg band. Recaptured birds were assigned a fat score without reference to previous records and their mass re-measured.

STOPOVER LENGTH AND RATE OF MASS CHANGE

The duration of stopover and rate of mass change were determined by analyzing recapture data from 1988 and 1989. Stopover length was conservatively calculated by subtracting the first capture date from the last capture date. The mass change of an individual was computed by subtracting the mass upon first capture from the mass upon last capture. The daily rate of mass change was

computed by dividing the change in mass by the length of stopover, which depends on an assumption of linear daily rates of gain. Because migrants show diel fluctuations in mass, the daily rate of change was standardized by computing the percent change/hr for each species, based on individuals recaptured on the same day. The percent/hr rates were then used to correct mass to 12:00 hr for all birds that were recaptured. Although changes in mass may reflect changes in the mass of flight musculature (Marsh 1984, Piersma 1990), the assumption was made that redeposition of fat accounted for essentially all mass gain of birds during stopover following trans-Gulf migration.

ESTIMATION OF FOOD AVAILABILITY

Our analysis of stopover focused on landbird migrants that rely principally on insects and other arthropods for food (Bent 1950, 1953). The relative density of food was estimated in 1988 and 1989 by sampling every third day throughout the spring field season using two techniques. The two sampling techniques were adopted to provide estimates that reflect food availability to insectivorous migrants.

Nonflying insects were sampled by clipping a 0.50 m branch from each of two trees at six sites randomly selected along a transect through each study site. The branch and associated leaves, petioles, and twigs were enclosed in a plastic bag, clipped from the tree and fumigated with insecticide. Later the contents were removed from the bag, the arthropods counted, sorted into five size-classes, and identified to order or family. Densities are expressed as numbers per standard branch (Fig. 2).

Flying insects were sampled at each of the six sampling sites by coating white 10 × 10 cm boards with Tanglefoot®, a sticky resin, and hanging them from the vegetation at 1.0, 1.5, and 2.0 m above the ground (see Hutto 1981). The boards were checked at 1.5 hr-intervals on sampling days. Insects were counted, sorted into size categories, and picked from the boards. The Tanglefoot® was smoothed and reapplied as necessary.

RESULTS

ARRIVAL CONDITION

A total of 874 birds of 49 species were captured and banded on ESI in 1987 (2,590.5 mist-net hours, 0.33 birds/net-hr). A greater netting effort

in 1988 (4,591.5 mist-net hours) and 1989 (4,261.8 mist-net hours) resulted in the capture of 3,352 birds (0.73 birds/net-hr) of 59 species and 3,097 (0.73 birds/net-hr) of 57 species, respectively.

Most birds captured in 1987 (78%), 1988 (64%) and 1989 (62%) had no visible subcutaneous fat and were given a fat class score of 0 (Fig. 3). The average body mass at first capture was near or below reported fat-free values for many species and, with the exception of Wood Thrushes (*Hyllocichla mustelina*), varied little between years (Table 1). The keel of the sternums of many individuals, notably Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) and *Catharus* thrushes, protruded conspicuously which suggests they had metabolized flight muscle during migration.

DURATION OF STOPOVER

Very few birds (3.0% of all migrants) were recaptured after the day of their first capture in 1987, while numbers were higher in 1988 (9.0%) and 1989 (12.5%). Most migrants that stopped on the island apparently departed the day of their arrival (first capture) or that night, although the proportion of birds recaptured at least one day following their arrival varied widely among species (Table 2). Birds that were recaptured on days following initial capture generally stayed two to three days (Table 2).

Lean birds occurred more frequently in samples of recaptured migrants. Figure 4 compares the distribution of fat scores among birds that were never recaptured with the distribution of fat scores among birds that were recaptured at least one day after initial capture on the island. The likelihood of recapture is related to the bird's energetic condition upon arrival in 1988 ($\chi^2 = 57$, $df = 2$, $P < 0.05$) and 1989 ($\chi^2 = 43$, $df = 2$, $P < 0.05$), but not in 1987 ($\chi^2 = 5.2$, $df = 2$, $P > 0.05$). The number of categories used to score visible fat reserves was collapsed to three (0, 1, and ≥ 2) for the contingency analysis.

How does length of stopover relate to arrival mass among individuals that stay beyond one day on ESI? Migrants of eight species were recaptured often enough, after combining 1988 and 1989 data, to examine the relationship between stopover length and arrival mass. Simple linear regression analysis revealed that the number of days a bird stayed on the island did not depend on arrival condition for any of the eight species (Table 3).

When the relationship between length of stay

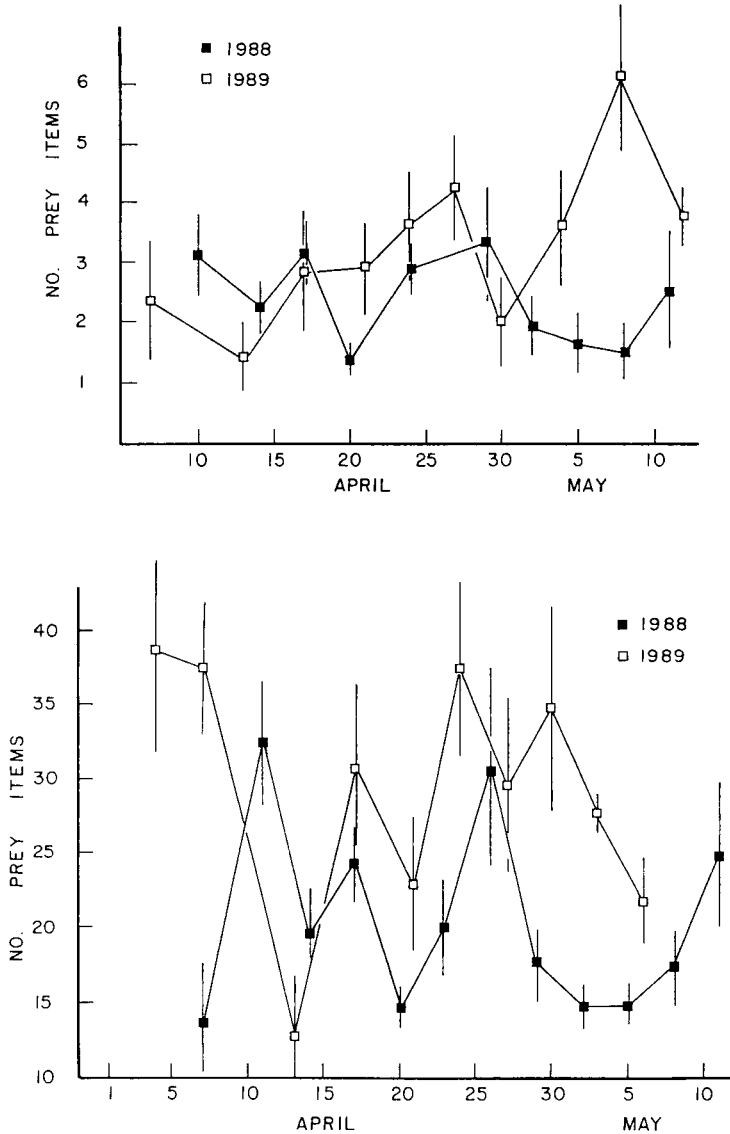


FIGURE 2. Upper: Mean (± 1 SE) number of prey items counted in branch samples from ESI in 1988 (closed squares) and 1989 (open squares) for each sampling date. Lower: Mean (± 1 SE) number of prey items captured on 10 x 10 cm sticky boards at six sites on ESI in 1988 (closed squares) and 1989 (open squares).

on ESI and change in mass is examined, individual variability characterized each species for which we have adequate samples (Fig. 5). Although the majority of individuals for many species lost mass in both 1988 and 1989 (Table 2), many individuals maintained their arrival mass, while some birds gained mass during stopover. Red-eyed Vireos (*Vireo olivaceus*), Rose-breasted Grosbeaks, and Summer Tanagers (*Piranga rubra*) were especially prone to losing mass dur-

ing stopover in 1988 and did so, on average, at high daily rates (Fig. 5).

Is the likelihood of gaining mass dependent on how long a migrant stayed on the island? On the one hand, rates of mass change for individuals that stayed only one day were lower than rates for individuals that stayed more than one day among several species in 1988 and 1989 (Tables 4 and 5). This difference is apparent, for example, when changes in mass are examined on an in-

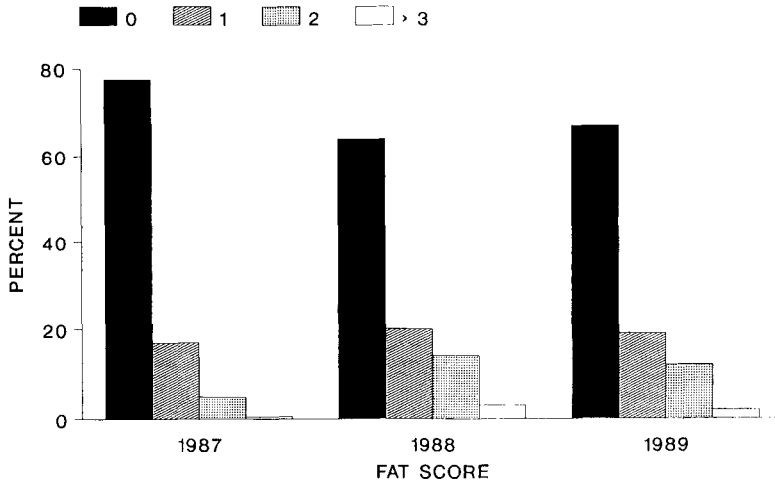


FIGURE 3. Distributions of fat scores for spring trans-Gulf migrants captured on East Ship Island in 1987, 1988 and 1989. Fat score classification derived from Helms and Drury 1960.

dividual basis for White-eyed Vireos (*Vireo griseus*) in both years and Red-eyed Vireos in 1988 (see Fig. 5); those individuals staying only one day lost mass.

Yet, change in mass does not increase linearly with stopover length. When we regressed change

in mass against length of stay, the slope of the regression line differed from zero for Rose-breasted Grosbeaks only, and then in the direction opposite from the expected positive slope (Table 3). The longer a Rose-breasted Grosbeak stayed on the island, the more mass it lost.

TABLE 1. Mean mass ± SD (*n*) for selected species captured on East Ship Island in 1987, 1988 and 1989 compared with fat-free values derived from published weights: Connell et al (1960),^a Rogers and Odum (1964),^b Rogers and Odum (1966).^c M = males, F = females, A = all birds.

Species	1987	1988	1989	Fat-free mass
American Redstart (M)	—	7.0 ± 0.7 (12)	7.2 ± 0.8 (20)	
<i>Setophaga ruticilla</i> (F)	6.8 ± 0.4 (10)	—	6.9 ± 0.7 (22)	6.94 (A) ^b
Bay-breasted Warbler (A)	—	10.9 ± 1.1 (16)	10.7 ± 1.2 (34)	9.88 (A) ^a
<i>Dendroica castanea</i>				
Chestnut-sided W. (A)	—	—	8.9 ± 1.0 (23)	8.16 (A) ^b
<i>Dendroica pennsylvanica</i>				
Magnolia Warbler (A)	7.1 ± 0.8 (22)	7.5 ± 0.6 (27)	7.5 ± 0.6 (79)	6.70 (A) ^a
<i>Dendroica magnolia</i>				
Tennessee Warbler (A)	—	—	8.2 ± 0.9 (60)	7.94 (A) ^a
<i>Vermivora peregrina</i>				
Northern Parula (A)	—	7.3 ± 1.3 (18)	6.8 ± 0.6 (13)	6.57 (A) ^b
<i>Parula americana</i>				
Prothonotary W. (M)	11.8 ± 0.9 (11)	12.4 ± 0.9 (11)	11.6 ± 1.0 (17)	
<i>Protonotaria citrea</i> (F)	—	11.9 ± 1.0 (33)	11.2 ± 0.8 (32)	11.56 (A) ^b
Indigo Bunting (M)	12.9 ± 1.3 (32)	14.2 ± 1.7 (200)	13.6 ± 1.5 (100)	13.14 (M) ^a
<i>Passerina cyanea</i> (F)	12.0 ± 1.5 (18)	12.8 ± 1.6 (159)	12.1 ± 1.4 (77)	12.46 (F) ^a
Scarlet Tanager (A)	23.9 ± 2.0 (23)	26.5 ± 3.1 (123)	25.8 ± 2.4 (45)	23.52 (A) ^a
<i>Piranga olivacea</i>				
Summer Tanager (A)	26.1 ± 2.3 (45)	26.3 ± 2.3 (94)	26.6 ± 2.5 (84)	24.13 (M) ^a
<i>Piranga rubra</i>				23.87 (F) ^a
Swainson's Thrush (A)	25.1 ± 2.8 (41)	24.3 ± 2.7 (139)	26.1 ± 2.6 (64)	26.22 (A) ^a
<i>Catharus ustulata</i>				
Wood Thrush (A)	39.2 ± 5.3 (18)	40.1 ± 3.8 (27)	45.0 ± 5.2 (34)	38.06 (A) ^c
<i>Hylocichla mustelina</i>				
Red-eyed Vireo (A)	15.0 ± 1.7 (170)	15.5 ± 1.6 (883)	15.6 ± 1.6 (638)	15.05 (M) ^a
<i>Vireo olivaceus</i>				14.55 (F) ^a

TABLE 2. The number (*n*) of recaptured birds (% of total captured given parenthetically), stopover length (SL), mass change (g/day) and per cent losing mass during stopover for selected species on East Ship Island in 1988 and 1989.

Species	1988				1989			
	<i>n</i> (%)	SL $\bar{x} \pm 1$ SD	g/d $\bar{x} \pm 1$ SD	% lost mass	<i>n</i> (%)	SL $\bar{x} \pm 1$ SD	g/d $\bar{x} \pm 1$ SD	% lost mass
<i>Miniotilta varia</i>	14 (22)	1.6 \pm 1.1	0.12 \pm 0.77	50	9 (21)	2.1 \pm 1.3	0.08 \pm 0.30	33
<i>Dendroica striata</i>	15 (22)	3.3 \pm 2.4	0.11 \pm 0.22	13	7 (19)	1.9 \pm 4.0	0.20 \pm 0.36	29
<i>Vermivora peregrina</i>	6 (10)	3.7 \pm 2.3	-0.05 \pm 0.29	50	7 (12)	2.9 \pm 1.6	-0.05 \pm 0.26	29
<i>Helmintheros vermivorus</i>	9 (22)	2.2 \pm 1.4	0.23 \pm 0.63	33	6 (8)	3.8 \pm 2.3	0.02 \pm 0.10	33
<i>Wilsonia citrina</i>					42 (34)	3.3 \pm 3.8	-0.04 \pm 0.26	42
<i>Vireo olivaceus</i>	29 (3)	1.9 \pm 1.9	-0.88 \pm 0.48	97	8 (1)	2.1 \pm 2.4	-0.56 \pm 0.49	88
<i>V. griseus</i>	30 (32)	3.2 \pm 2.9	0.00 \pm 0.46	57	38 (16)	4.4 \pm 3.9	-0.11 \pm 0.29	66
<i>Passerina cyanea</i>	31 (9)	3.5 \pm 3.7	-0.10 \pm 0.58	55	13 (7)	2.8 \pm 2.0	-0.26 \pm 0.52	62
<i>P. ciris</i>	11 (22)	2.5 \pm 2.1	-0.09 \pm 0.45	64				
<i>Phenicicus ludovicianus</i>	21 (12)	1.9 \pm 1.6	-2.21 \pm 1.52	95				
<i>Icterus spurius</i>	19 (12)	1.8 \pm 1.2	0.55 \pm 0.71	21	17 (14)	3.4 \pm 1.9	-0.22 \pm 0.47	59
<i>Piranga rubra</i>	8 (9)	1.7 \pm 1.5	-1.61 \pm 1.54	88	6 (7)	2.3 \pm 2.0	-0.96 \pm 0.89	100
<i>Catharus minimus</i>	11 (13)	2.6 \pm 2.4	0.19 \pm 0.75	27				
<i>C. ustulatus</i>	12 (9)	1.5 \pm 1.1	-0.74 \pm 1.20	83				
<i>Dumetella carolinensis</i>	14 (10)	4.2 \pm 4.0	-0.10 \pm 0.33	64	21 (13)	4.7 \pm 6.0	-0.41 \pm 1.10	67

RATE OF MASS CHANGE

Most species that stopped on ESI were characterized by negative rates of change in mass (Table 2). Rates varied between -2.21 g/day for Rose-breasted Grosbeaks to +0.55 g/day for Orchard Orioles in 1988. Only Blackpoll Warblers (*Dendroica striata*), Worm-eating Warbler (*Helmintheros vermivorus*), Orchard Oriole (*Icterus spurius*), and Gray-cheeked Thrush (*Catharus minimus*) gained mass at a rate that would, on average, result in a measurable replenishment of fat. Variation in average rates of mass change among the 10 species with samples from both years (Table 2) was analyzed as a two-way ANOVA, without replication (Zar 1984). Average rates of mass change did not differ between years ($F = 0.16$, $df = 1, 9$, $P > 0.05$), but did differ among species ($F = 5.55$, $df = 1, 9$, $P < 0.05$).

BETWEEN-YEAR COMPARISON

Prey numbers tended to be higher over the first week in May in 1989, otherwise our estimates of prey abundance did not differ between the two seasons on ESI. Assuming that food availability affects length of stopover and rate of gain and given little, if any, difference in food availability between years, we would not expect stopover length and rate of mass change to differ between 1988 and 1989 (Table 3). With the exception of Orchard Orioles, which stayed a shorter time ($P < 0.01$) and gained mass more rapidly ($P < 0.01$) in 1988, other species for which adequate samples permitted comparison (see Table 2; Fig. 5) did not differ in length of stay. A two-way ANOVA, without replication, of average rates of change (g/d) for the same 10 species in 1988 and 1989 did not reveal a between-year effect for either stopover length ($F = 1.00$, $df = 1, 9$, $P > 0.05$) or rate of mass change ($F = 0.16$, $df = 1, 9$, $P > 0.05$). Moreover, the qualitative relationship between stopover length and rate of mass change was not consistent among species: Four species averaged longer stopover the year their rate of gain was higher (e.g., Black-and-White Warbler, *Mniotilta varia*), while five species stayed longer the year their rate declined (e.g., Orchard Oriole).

ARRIVAL MASS AND RATE OF MASS CHANGE

Some of the individual variability in rate of mass change (see Fig. 5) can be explained by the bird's energetic condition following trans-Gulf migration. When rate of gain (g/d) is regressed against

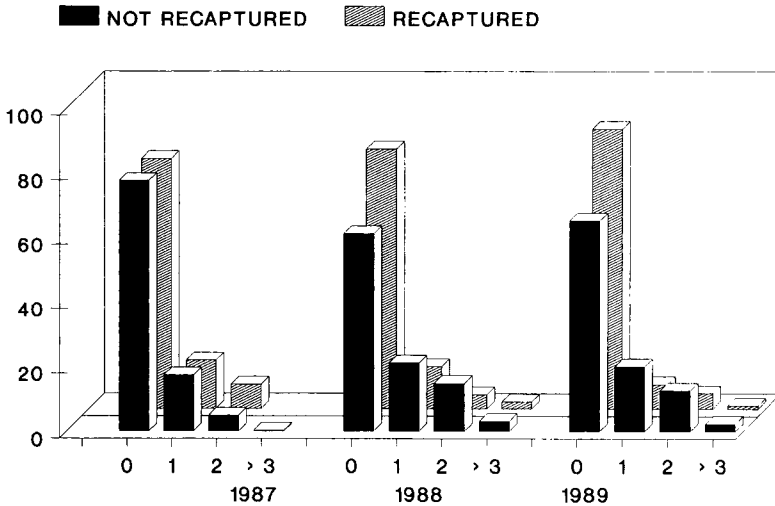


FIGURE 4. Distributions of fat scores of recaptured trans-Gulf migrants and migrants that were never recaptured on East Ship Island in 1987, 1988, and 1989.

arrival mass, the slope of the best fit line is negative ($P < 0.05$) for five of the eight species examined (Fig. 6), i.e., rate of fat deposition is positively related to energy demand. Although only a small fraction of the variation in rate of gain is explained by arrival mass, low coefficients of determination are not surprising given the different variables that probably influence rates of mass change during stopover (e.g., Rappole and Warner 1976, Mehlum 1983b, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Safriel and Lavee 1988).

DISCUSSION

ARRIVAL CONDITION

Most of the migrants that stopped on East Ship Island arrived near or below fat-free mass. The possible consequences of arriving in a fat-de-

pleted condition are several. (1) Lean migrants have a smaller "margin of safety" to buffer the effect of adverse weather on the availability of food supplies during stopover (Nisbet and Drury 1968; cf. Rogers 1987). (2) Efforts to satisfy energy demand may expose fat-depleted migrants to increased predation pressure (Metcalf and Furness 1984; Lindström 1989, 1990; see review, Lima and Dill 1990). (3) If lean birds remain longer at stopover sites than birds in better energetic condition (Bairlein 1985, Pettersson and Hasselquist 1985, Biebach et al. 1986, Moore and Kerlinger 1987) and do not make up the lost time, they will necessarily arrive later on the breeding grounds (Lavee and Safriel 1989). Migrants that arrive late on the breeding grounds might experience difficulty securing a high quality territory and or attracting a mate.

TABLE 3. Results of linear regression analyses of the relationship between (a) stop over length (SL) and arrival condition and (b) change in mass and stopover length for Neotropical landbird migrants that stop over on East Ship Island following trans-Gulf migration. Two-tailed probability (P) is given. See Tables 1 and 2 for scientific names.

Species	n	SL vs. arrival mass			Mass change vs. SL		
		r ²	Slope (b)	P	r ²	Slope (b)	P
Black-and-White W.	23	0.02	-0.24	0.52	0.09	0.25	0.17
Blackpoll Warbler	22	0.07	0.74	0.25	0.16	0.09	0.07
Red-eyed Vireo	37	0.09	0.46	0.07	0.02	-0.04	0.52
White-eyed Vireo	68	0.01	-0.19	0.68	0.01	-0.02	0.49
Summer Tanager	14	0.11	-0.27	0.25	0.02	0.15	0.67
Orchard Oriole	35	0.01	-0.07	0.73	0.03	-0.10	0.33
Rose-breasted Grosbeak	25	0.04	0.16	0.32	0.29	-0.68	<0.01
Indigo Bunting	44	0.03	-0.33	0.29	0.07	0.07	0.09

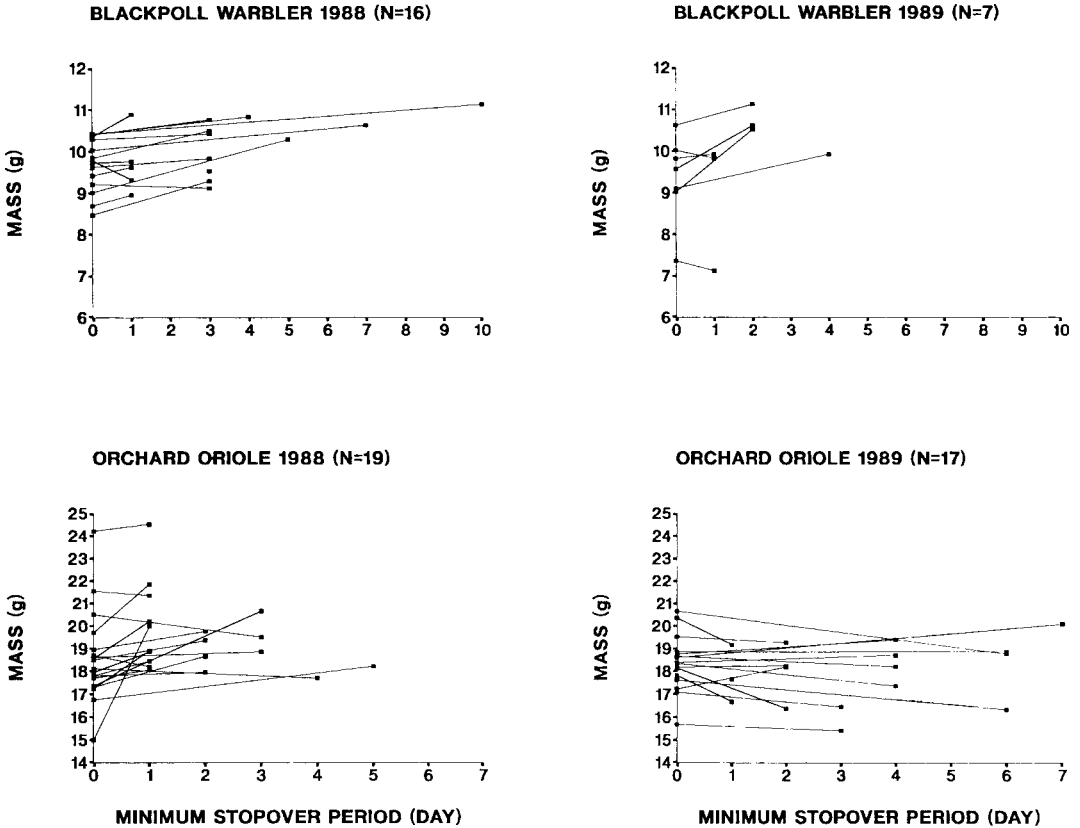


FIGURE 5. Species-specific changes in mass for recaptured migrants on East Ship Island. Each line connects mass upon first capture to mass at last recapture and represents one individual.

Although we assume that weight differences among birds on the island reflect differences in fat stores, other factors may contribute to the reduced mass of some migrants. Long, nonstop flights over ecological barriers might dehydrate migrants (Wood 1982, Biebach 1990) which would depress body mass (e.g., Karlsson et al. 1988). Yet, Swainson's Thrushes (*Catharus ustulatus*) were not significantly dehydrated following trans-Gulf migration (Child 1969), and a difference in water content was not responsible for differences in body mass between European Robins (*Erithacus rubecula*) flying overland and those grounded after an extensive flight over the Baltic Sea (Åkesson et al., in press).

Body mass would also decline if muscle tissue is catabolized during long, nonstop flights. Hypertrophy of flight musculature contributes to increased pre-migratory body mass (e.g., Fry et al. 1972, Marsh 1984), and birds could use muscle protein to supplement energy supplies during

periods of environmental and physiological stress (cf. Piersma and Jukema 1990, Piersma 1990). Moreover, once the Gulf of Mexico is crossed, the selective pressure for enlarged flight musculature might be relaxed.

STOPOVER DURATION AND RATE OF MASS CHANGE

The combination of low fat reserves coupled with a high probability of rebuilding reserves should induce a migrant to stay at a stopover site. Low fat combined with a low probability of replenishment should favor departure and the search for more suitable stopover habitat (Rappole and Warner 1976, Graber and Graber 1983, Biebach 1985, Gwinner et al. 1985, Terrill 1988, Alerstam and Lindström 1990). Migrants might leave ESI because they experience few opportunities to satisfy energy demand.

First, most migrants were never recaptured on ESI and presumably departed shortly after they

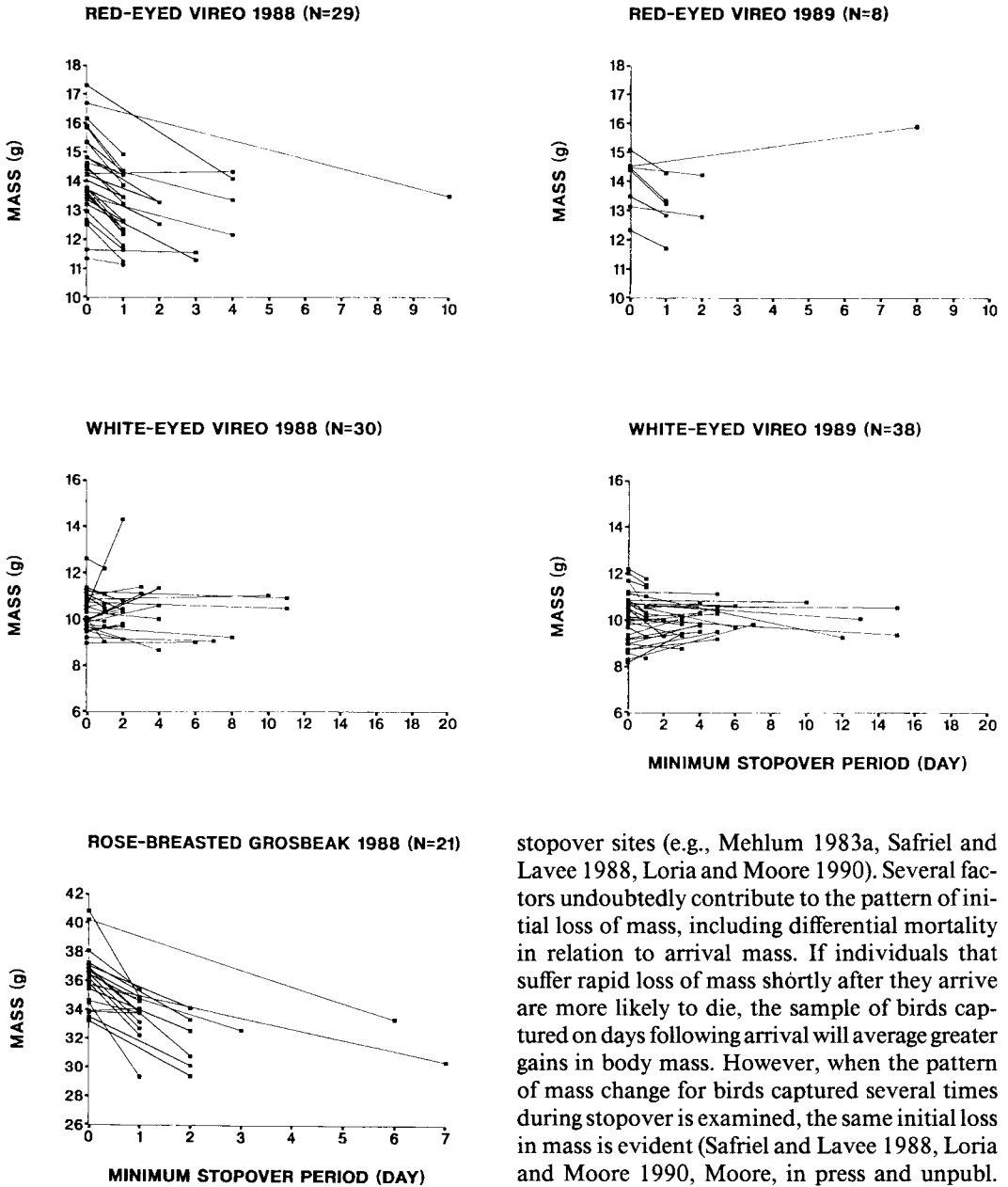


FIGURE 5. Continued.

arrived, regardless of arrival condition. Length of stay on ESI was not directly related to greater gain in body mass, which probably explains why stopover length was not related to arrival mass among migrants. It is true that migrants staying more than one day gained more mass or lost less mass than birds staying only one day. A pattern of initial mass loss has been reported at other

stopover sites (e.g., Mehlum 1983a, Safriel and Lavee 1988, Loria and Moore 1990). Several factors undoubtedly contribute to the pattern of initial loss of mass, including differential mortality in relation to arrival mass. If individuals that suffer rapid loss of mass shortly after they arrive are more likely to die, the sample of birds captured on days following arrival will average greater gains in body mass. However, when the pattern of mass change for birds captured several times during stopover is examined, the same initial loss in mass is evident (Safriel and Lavee 1988, Loria and Moore 1990, Moore, in press and unpubl. data). Possibly only those migrants able to defend adequate food sources (i.e., acquire temporary territories) stay and gain mass (e.g., Rappole and Warner 1976). It is also likely that a migrant must familiarize itself with stopover habitat before it can forage effectively and expect to gain mass (Moore et al. 1990). If migrants regard ESI to be less than the best place to replenish depleted reserves, many might depart in search of a better location.

TABLE 4. Rates of mass change for migrants staying either one day or longer than one day on East Ship Island, 1988. One-tailed *P* values reported. See Tables 1 and 2 for scientific names.

Species	Length of stopover				<i>t</i> -test <i>P</i>
	1 Day		>1 Day		
	g/day ± 1 SD	<i>n</i>	g/day ± 1 SD	<i>n</i>	
Black-and-White Warbler	-0.52 ± 0.50	8	0.43 ± 0.75	6	<0.01
Blackpoll Warbler	0.10 ± 0.39	5	0.12 ± 0.10	11	NS
Red-eyed Vireo	-1.12 ± 0.37	19	-0.43 ± 0.29	10	<0.001
White-eyed Vireo	-0.29 ± 0.35	9	0.12 ± 0.09	21	<0.01
Indigo Bunting	-0.19 ± 0.94	10	-0.03 ± 0.37	10	NS
Painted Bunting	-0.36 ± 0.52	5	0.12 ± 0.24	6	<0.05
Rose-breasted Grosbeak	-2.66 ± 1.84	12	-1.61 ± 0.65	9	<0.05
Orchard Oriole	0.79 ± 0.85	10	0.29 ± 0.43	9	NS
Thrushes ^a	-0.62 ± 1.22	15	0.05 ± 0.72	14	<0.05

^a The rate of change for individual Gray-cheeked Thrushes (*n* = 11), Swainson's Thrush (*n* = 12) and Veerys (*n* = 6) were combined to obtain the *Catharus* Thrush values.

Second, as lipid stores are depleted during migration, free-ranging birds are capable of rebuilding reserves in a few days at rates approaching 10% body mass/day (e.g., Dolnik and Blyumental 1967, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Dolnik 1990, Lindström, in press). Migrants on ESI failed to achieve positive, let alone very rapid, rates of gain in either 1988 or 1989. Alerstam and Lindström (1990) argue that the stopover decision for maximizing speed of migration depends on the migrant's arrival condition (fat status) and expected rate of fat deposition. When even a lean migrant experiences a very low rate of fat deposition during stopover, the best decision might be to move on (e.g., Rappole and Warner 1976, Graber and Graber 1983).

If food availability affects the rate at which migrants restore depleted energy reserves, migrants should experience higher fat deposition rates in years when food is more abundant (see Moore and Simons, in press). For example, Sedge Warblers (*Acrocephalus schoenobaenus*) gained 0.40 and 0.55 g/day in 1973 and 1975, respectively, in a French marshland near Le Migron,

but only 0.05 g/day when aphid abundance was very low in 1974 (Bibby et al. 1976). Year-to-year differences in the rate of mass change among European Robins at an island study site along the Skagerrak coast during fall migration were thought to be related to food availability (Mehlum 1983a). The rate of food consumption by passage wood-warblers varied with the supply of lepidopterous larvae during a three year (1979–1981) study of spring migration in southern Illinois (Graber and Graber 1983). Because our estimates of food availability did not differ between years, we did not expect differences in rate of mass change. The fact that we did not observe any differences requires us to draw an inference from negative results.

We did find that rate of mass change was related to arrival mass (presumptive energy demand), which is consistent with the notion that fat-depleted migrants compensate for heightened energy demand (Loria and Moore 1990). If passage migrants are selected to minimize time spent migrating (Alerstam and Lindström 1990), it is reasonable to expect the evolution of compensatory mechanisms to meet nutritional demands

TABLE 5. Rates of mass change for migrants staying either one day or longer than one day on East Ship Island in 1989. One-tailed *P* values reported. See Tables 1 and 2 for scientific names.

Species	Length of stopover				<i>t</i> -test <i>P</i>
	1 Day		>1 Day		
	g/day ± 1 SD	<i>n</i>	g/day ± 1 SD	<i>n</i>	
Hooded Warbler	-0.04 ± 0.28	20	-0.05 ± 0.24	22	NS
White-eyed Vireo	0.41 ± 0.27	11	0.01 ± 0.18	27	<0.01
Indigo Bunting	-0.54 ± 0.71	5	-0.08 ± 0.29	8	NS
Gray Catbird	-1.17 ± 1.40	8	0.03 ± 0.62	15	<0.05

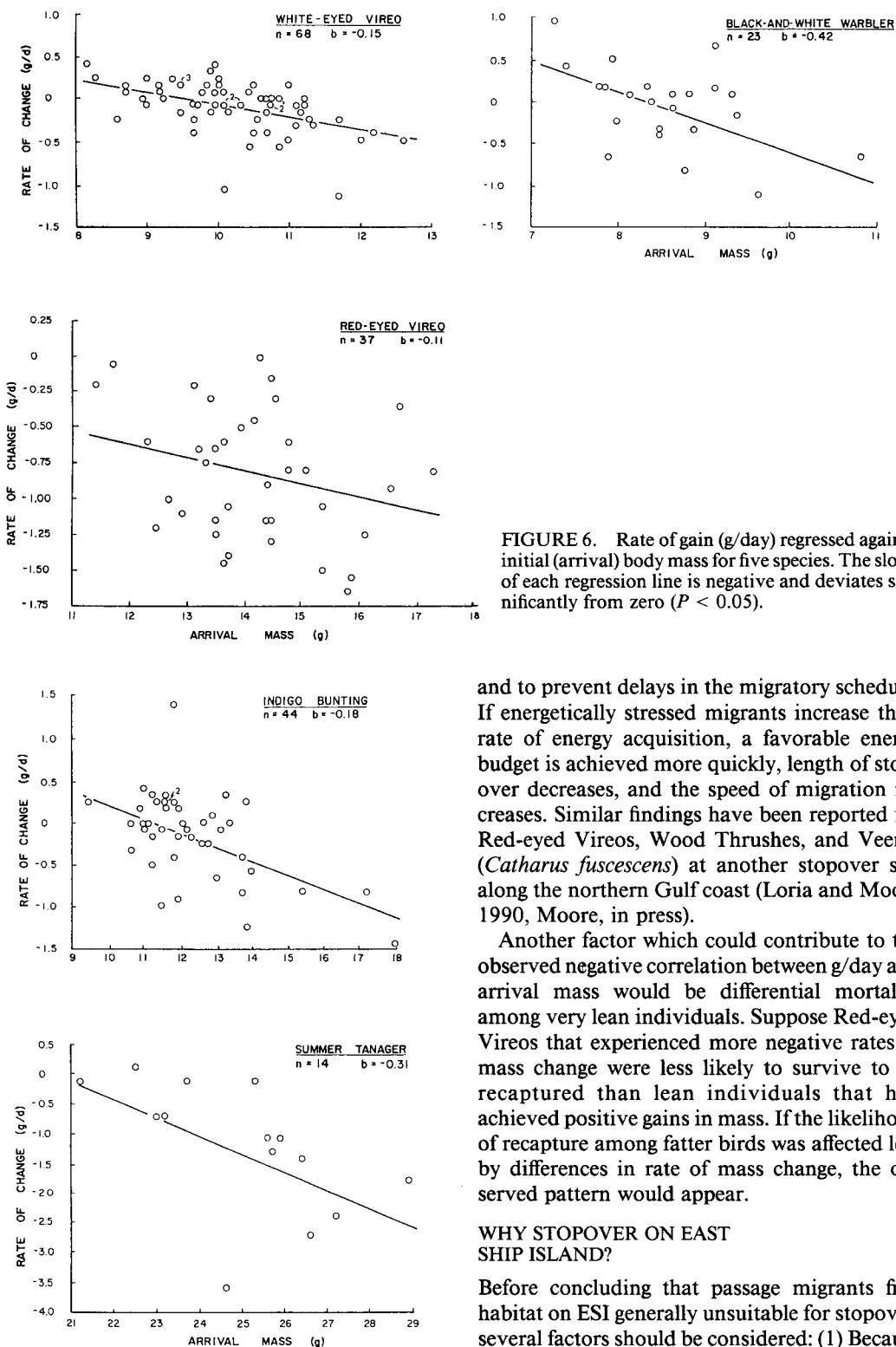


FIGURE 6. Rate of gain (g/day) regressed against initial (arrival) body mass for five species. The slope of each regression line is negative and deviates significantly from zero ($P < 0.05$).

and to prevent delays in the migratory schedule. If energetically stressed migrants increase their rate of energy acquisition, a favorable energy budget is achieved more quickly, length of stopover decreases, and the speed of migration increases. Similar findings have been reported for Red-eyed Vireos, Wood Thrushes, and Veerys (*Catharus fuscescens*) at another stopover site along the northern Gulf coast (Loria and Moore 1990, Moore, in press).

Another factor which could contribute to the observed negative correlation between g/day and arrival mass would be differential mortality among very lean individuals. Suppose Red-eyed Vireos that experienced more negative rates of mass change were less likely to survive to be recaptured than lean individuals that had achieved positive gains in mass. If the likelihood of recapture among fatter birds was affected less by differences in rate of mass change, the observed pattern would appear.

WHY STOPOVER ON EAST SHIP ISLAND?

Before concluding that passage migrants find habitat on ESI generally unsuitable for stopover, several factors should be considered: (1) Because

species-specific rates of mass change were calculated by averaging individual rates of change, a species may have a negative daily rate, though not all individuals lost mass during their stay. A negative daily rate of change also obtains when birds with a shorter stopover duration lose mass, whereas those with a longer stopover duration gain mass. Consequently, the contribution of birds that gain mass to the daily mean is relatively low when calculating a mean daily rate of mass change. In addition to individual variability, differences in rates of mass change among species suggest that certain species (e.g., Black-poll Warblers) utilize habitat on ESI more effectively than other species and successfully replenish energy reserves. Although not the subject of the current study, this possibility is consistent with the occurrence of species-specific patterns of habitat use during migration (e.g., Bairlein 1983, Moore et al. 1990, Dolnik 1990) and warrants greater attention.

(2) Substantial gains in mass and large fat loads might not be expected following trans-Gulf migration even under the best of stopover conditions (cf. Caldwell et al. 1963, Johnston 1966). Because flight costs increase as the fat load accumulates (e.g., Alerstam 1979), a migrant's flight range becomes a negatively accelerated function of its fat reserves (see Alerstam and Lindström 1990). The large fat stores which provide a margin of safety during long distance, nonstop flights over ecological barriers would not be necessary for overland flight (cf. Sandberg et al. 1988, Moore and Kerlinger, in press).

Heavy fat loads might impose additional costs during migration. Besides the energetic costs of fat accumulation, the added weight of fat reserves adversely affects flight performance (e.g., Blem 1975, Andersson and Norberg 1981) and increases the risk of predation (e.g., Steube and Ketterson 1982, Nolan and Ketterson 1983, Lima 1986).

(3) Factors other than food availability and the likelihood of replenishing energy reserves affect the intrinsic suitability of habitat and stopover decisions (Alerstam and Lindström 1990, Moore and Simons, in press). Whereas dehydration does not appear to be a serious en route problem for small landbird migrants (Haas and Beck 1979, Biebach 1990), water economy might constrain migratory range and could explain why some individuals stopped on the island despite sufficient

reserves for continued migration (Nachtigall 1990). Moreover, lean migrants that have mobilized carbohydrate or protein sources while crossing the Gulf of Mexico might experience a more serious water balance problem than birds that have relied solely on their lipid reserves.

Predation probably constitutes a significant hazard to migrants (e.g., Lindström 1989) and stopover habitats may vary in terms of predation risks (e.g., Moore et al. 1990, Lindström 1990). When the best areas for depositing fat are also the most dangerous, the migrant must trade off energy gain against mortality risks (cf. Lima and Dill 1990). For example, migrating Bramblings (*Fringilla montifringilla*) often shift from rape fields, where both energy gain and predation pressure are high, to Beech forests, where energy gain and predation risk are low, in years of beech mast (Lindström 1989).

Despite higher oxidative capacity in migratory birds (Lundgren and Kiessling 1985, Lundgren 1988), migrants might suffer muscular fatigue during sustained flight over ecological barriers and might stop over to metabolize lactate and "repay" an oxygen debt, regardless of their fat status. Stopover would also be required for tissue repair if migrants are forced to catabolize muscle tissue to offset unexpected energy demands (see Piersma 1990) or if muscle fibers are damaged during sustained, long-distance flight across the Gulf of Mexico. In either case, a safe place to rest may be an important determinant of suitability as food availability.

(4) Finally, factors extrinsic to stopover habitat influence stopover decisions (Hutto 1985a, Moore and Simons, in press). How effectively migrants satisfy energy demands and meet en route contingencies depends, for example, on (a) the time and energy available for selecting among alternative habitats, (b) the relative availability of more suitable habitats, (c) the migrant's searching efficiency and (d) the probability of survival during migration (cf. Ward 1987). Favorable en route habitat is probably limited effectively for migrants because migrants do not have the luxury of searching for the "best" stopover site. For the fat-depleted bird that is unfamiliar with the availability of favorable stopover habitat following trans-Gulf migration, the benefits of rejecting what appears to be less suitable habitat on ESI may be outweighed by the cost of finding a more suitable site.

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LITERATURE CITED

- ÅKESSON, S., L. KARLSSON, J. PETTERSSON, AND G. WALINDER. In press. Body contents and migration strategies: a comparison between Robins *Erithacus rubecula* from two stop-over sites in Sweden. *Die Vogelwarte*.
- ALERSTAM, T. 1979. Wind as a selective agent in bird migration. *Ornis Scand.* 10:76-93.
- ALERSTAM, T. 1981. The course and timing of bird migration, p. 9-54. In D. J. Aidley [ed.], *Animal migration*. Cambridge University Press, Cambridge, U.K.
- ALERSTAM, T. 1990. Ecological causes and consequences of bird orientation. *Experientia* 46:405-415.
- ALERSTAM, T., AND Å. LINDSTRÖM. 1990. Optimal bird migration: the relative importance of time, energy, and safety, p. 311-351. In E. Gwinner [ed.], *Bird migration*. Springer-Verlag, Berlin.
- ANDERSSON, M., AND R. Å. NORBERG. 1981. Evolution of reversed size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* 15: 105-130.
- BAIRLEIN, F. 1983. Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations. *Ornis Scand.* 14:239-245.
- BAIRLEIN, F. 1985. Body weights and fat deposition of Palaearctic passerine migrants in the central Sahara. *Oecologia* 66:141-146.
- BENT, A. C. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. *Bull. U.S. Natl. Mus.* 197.
- BENT, A. C. 1953. Life histories of North American wood warblers. *Bull. U.S. Natl. Mus.* 203.
- BIBBY, C. F., AND R. E. GREEN. 1983. Food and fattening of migrating warblers in some French marshlands. *Ring. & Migr.* 4:175-184.
- BIBBY, C. F., R. E. GREEN, G. R. M. PEPLER, AND P. A. PEPLER. 1976. Sedge warbler migration and reed aphids. *Br. Birds* 69:384-399.
- BIEBACH, H. 1985. Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experientia* 41:695-697.
- BIEBACH, H. 1990. Strategies of trans-Saharan migrants, p. 352-367. In E. Gwinner [ed.], *Bird migration*. Springer-Verlag, Berlin.
- BIEBACH, H., W. FRIEDRICH, AND G. HEINE. 1986. Interaction of body mass, fat, foraging and stop-over period in trans-Saharan migrating passerine birds. *Oecologia* 69:370-379.
- BLEM, C. R. 1975. Geographic variation in wing-loading of the House Sparrow. *Wilson Bull.* 87: 543-549.
- CALDWELL, L. D., E. P. ODUM, AND S. G. MARSHALL. 1963. Comparison of fat levels in migrating birds killed at a central Michigan and a Florida Gulf Coast television tower. *Wilson Bull.* 75:428-434.
- CHILD, G. I. 1969. A study of nonfat weights in migrating Swainson's Thrushes (*Hylocichla ustulata*). *Auk* 86:327-338.
- CONNELL, C., E. ODUM, AND H. KALE. 1960. Fat-free weights of birds. *Auk* 77:1-9.
- DOLNIK, V. R. 1990. Bird migration across arid and mountainous regions of Middle Asia and Kazakhstan, p. 368-386. In E. Gwinner [ed.], *Bird migration*. Springer-Verlag, Berlin.
- DOLNIK, V. R., AND T. I. BLYUMENTAL. 1967. Autumnal premigratory and migratory periods in the Chaffinch (*Fringilla coelebs coelebs*) and some other temperate zone birds. *Condor* 69:435-468.
- FRY, C. H., I. J. FERGUSON-LEES, AND R. J. DOWSETT. 1972. Flight muscle hypertrophy and ecophysiological variation of Yellow wagtail *Motacilla flava* races at Lake Chad. *J. Zool., Lond.* 167:293-306.
- GRABER, J. W., AND R. R. GRABER. 1983. Feeding rates of warblers in spring. *Condor* 85:139-150.
- GWINNER, E., H. BIEBACH, AND I. KREIS. 1985. Food availability affects migratory restlessness in Garden Warblers (*Sylvia borin*). *Naturwissenschaften* 72:51-52.
- HAAS, W., AND P. BECK. 1979. Zum Frühjahrsvogelzug palaarktischer Vogel über die westliche Sahara. *J. Ornithol.* 120:237-246.
- HELMS, C. W., AND W. H. DRURY. 1960. Winter and migratory weight and fat: field studies on some North American buntings. *Bird-Banding* 31:1-40.
- HUTTO, R. L. 1981. Temporal patterns of foraging activity in some Wood Warblers in relation to the activity at insect prey. *Behav. Ecol. Sociobiol.* 9: 195-198.
- HUTTO, R. L. 1985a. Habitat selection by nonbreeding, migratory land birds, p. 455-476. In M. Cody [ed.], *Habitat selection in birds*. Academic Press, New York.
- HUTTO, R. L. 1985b. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? *Auk* 102:120-132.
- JOHNSTON, D. W. 1966. A review of the vernal fat deposition picture in overland migrant birds. *Bird-Banding* 37:172-183.
- KARLSSON, L., K. PERSSON, J. PETTERSSON, AND G. WALINDER. 1988. Fat-weight relationships and migratory strategies in the Robin *Erithacus rubecula* at two stop-over sites in South Sweden. *Ring. & Migr.* 9:160-168.

- LAVEE, D., AND S. SAFRIEL. 1989. The dilemma of cross-desert migrants—stopover or skip a small oasis? *J. Arid Environ.* 17:69–81.
- LIMA, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377–385.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68:619–640.
- LINDSTRÖM, Å. 1989. Finch flock size and risk of hawk predation at a migratory stopover site. *Auk* 106:225–232.
- LINDSTRÖM, Å. In press. Maximum fat deposition rates in migrating birds. *Ornis Scand.*
- LINDSTRÖM, Å. The role of predation risk in stopover habitat selection in migrating Bramblings *Fringilla montifringilla*. *Behav. Ecol.* 1:102–106.
- LINDSTRÖM, Å., AND T. ALERSTAM. 1986. The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. Montifringilla* during autumn in southern Sweden. *Behav. Ecol. Sociobiol.* 19:417–424.
- LORIA, D. E., AND F. R. MOORE. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behav. Ecol.* 1:24–35.
- LUNDGREN, B. O., AND K.-H. KIESSLING. 1985. Seasonal variation in catabolic enzyme activities in breast muscle of some migratory birds. *Oecologia* 66:468–471.
- LUNDGREN, B. 1988. Catabolic enzyme activities in the pectoralis muscle of migratory and nonmigratory Goldcrests, Great Tits and Yellowhammers. *Ornis Scand.* 19:190–194.
- MARSH, R. L. 1984. Adaptations of the Gray Catbird *Dumetella carolinensis* to long-distance migration: flight muscle hypertrophy associated with elevated body mass. *Physiol. Zool.* 57:105–117.
- MARTIN, T. E. 1980. Diversity and abundance of spring migratory birds using habitat islands on the Great Plains. *Condor* 82:430–439.
- MARTIN, T. R., AND J. R. KARR. 1986. Patch utilization by migrating birds: resource oriented? *Ornis Scand.* 17:165–174.
- MEHLUM, F. 1983a. Weight changes in migrating Robins (*Erithacus rubecula*) during stop-over at the island of Store Faeder, Outer Oslofjord, Norway. *Fauna norv. Ser. C, Cinclus* 6:57–61.
- MEHLUM, F. 1983b. Resting time in migrating Robins (*Erithacus rubecula*) during stop-over at the island of Store Faeder, Outer Oslofjord, Norway. *Fauna norv. Ser. C, Cinclus* 6:62–72.
- METCALFE, N. B., AND R. W. FURNESS. 1984. Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. *Behav. Ecol. Sociobiol.* 15:203–206.
- MILLER, G. J. 1975. Vegetation dynamics on Ship Island, Mississippi. Ph.D. diss. Univ. Georgia, Athens, GA.
- MOORE, F. R. In press. Ecophysiological and behavioral response to energy demand during migration. *Proc. XXth Int. Ornithol. Congr.*
- MOORE, F. R., AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47–54.
- MOORE, F. R., AND P. KERLINGER. In press. Nocturnality, long-distance migration, and ecological barriers. *Proc. XXth Int. Ornithol. Congr.*
- MOORE, F. R., AND T. E. SIMONS. In press. Habitat suitability and the stopover ecology of Neotropical landbird migrants. In J. Hagan and D. Johnston [eds.], *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Inst. Press, Washington, DC.
- MOORE, F. R., AND W. YONG. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behav. Ecol. Sociobiol.* 28: 85–90.
- MOORE, F. R., P. KERLINGER, AND T. R. SIMONS. 1990. Stopover on a Gulf coast barrier island by spring trans-Gulf migrants. *Wilson Bull.* 102:487–500.
- NACHTIGALL, W. 1990. Wind tunnel measurements of long-time flights in relation to the energetics and water economy of migrating birds, p. 319–327. In E. Gwinner [ed.], *Bird migration*. Springer-Verlag, Berlin.
- NISBET, I., AND W. H. DRURY. 1968. Short-term effects of weather on bird migration: a field study using multivariate statistics. *Anim. Behav.* 16:496–530.
- NOLAN, V., AND E. KETTERSON. 1983. An analysis of body mass, wing length, and visible fat deposits of Dark-eyed Juncos wintering at different latitudes. *Wilson Bull.* 95:603–620.
- PETTERSSON, J., AND D. HASSELQUIST. 1985. Fat deposition and migration capacity of Robins *Erithacus rubecula* and Goldcrest *Regulus regulus* at Ottenby, Sweden. *Ringing & Migr.* 6:66–75.
- PIERSMA, T. 1990. Pre-migratory “fattening” usually involves more than the deposition of fat alone. *Ringing & Migr.* 11:113–115.
- PIERSMA, T., AND J. JUKEMA. 1990. Budgeting the flight of a long-distance migrant: changes in nutrient levels of Bar-tailed Godwits at successive spring staging sites. *Ardea* 78:315–338.
- RAPPOLE, J. H., AND D. W. WARNER. 1976. Relationships between behavior, physiology and weather in avian transients at a migration stopover site. *Oecologia* 26:193–212.
- ROGERS, C. M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology* 68:1051–1061.
- ROGERS, D. T., AND E. P. ODUM. 1964. Effect of age, sex, and level of fat deposition on major body components in some wood warblers. *Auk* 81:505–513.
- ROGERS, D. T., AND E. P. ODUM. 1966. A study of autumnal postmigrant weights and vernal fattening of North American migrants in the tropics. *Wilson Bull.* 78:415–433.
- SAFRIEL, U. N., AND D. LAVEE. 1988. Weight changes of cross-desert migrants at an oasis—do energetic considerations alone determine the length of stopover? *Oecologia* 76:611–619.
- SANDBERG, R., J. PETTERSSON, AND T. ALERSTAM. 1988. Why do migrating robins, *Erithacus rubecula*, captured at two nearby stop-over sites orient differently? *Anim. Behav.* 36:865–876.
- STUEBE, M. M., AND E. D. KETTERSON. 1982. A study of fasting in Tree Sparrows (*Spizella arborea*) and

- Dark-eyed Juncos (*Junco h. hyemalis*): ecological implications. *Auk* 99:299–308.
- TERRILL, S. B. 1988. The relative importance of ecological factors in bird migration. *Proc. XIX Int. Ornithol. Congr.* (1988):2180–2190.
- WARD, S. A. 1987. Optimal habitat selection in time-limited dispersers. *Am. Nat.* 129:568–579.
- WOOD, B. 1982. The trans-Saharan spring migration of yellow wagtails (*Motacilla flava*). *J. Zool., Lond.* 197:267–283.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.